A population assessment and distribution of the endemic Enid snail *Pachnodus fregatensis* on Frégate Island, Seychelles

Tatiana Raposo de Rezende & Gregory Canning
Frégate Island Private, Ecology Department
P.O. Box 330, Victoria, Mahé, SEYCHELLES
[*mariatatifox@hotmail.com*]

Abstract: The Frégate Island Enid snail *Pachnodus fregatensis* is a terrestrial mollusc endemic to an island of $2km^2$ in the Seychelles and is classified as an Endangered species according to the IUCN Red List. Previous assessments revealed a substantial decline in the population following a successful rat eradication programme in 2001 as a result of susceptibility to the poison used. In 2002, the snail population was estimated at 7700 individuals and the latest estimate reveals a significant increase to 63890 individuals as well as dispersal into previously unrecorded habitat.

Key words: Enid snail, terrestrial mollusc, island, population trend, Cerastidae

Introduction

Terrestrial snails, being a major component of oceanic island biota, offer much in terms of answering questions of evolution and biogeography (Holland & Cowie 2009). However, before their value in evolutionary biology can be determined, basic information, such as their conservation status, population size and ecological requirements need to be determined. Most animal conservation efforts are directed at vertebrates, even though these animals represent only about 1% of the extant biodiversity (Ponder & Lunney 1999). This contrasts with the current extinction risk among invertebrates, less than 0.3% of which has been evaluated for cataloguing in the IUCN lists (Baillie *et al*. 2004). Molluscs represent the group with the highest number of recorded extinctions, and terrestrial molluscs are especially prone to disappearance as they include many endemics with restricted distributions and limited dispersal capacity (Lydeard *et al*. 2004).

The Frégate Island Enid Snail *Pachnodus fregatensis* (Van Mol & Coppois, 1980) is no exception. It is a terrestrial species that occupies a single, continuous range of only two square kilometres on Frégate Island in the Seychelles archipelago. *Pachnodus fregatensis* is classified as Endangered on the IUCN Red List of Threatened Species with the population trend being unknown (category A1a) (2011). As with other threatened species, it has been neglected in ecological studies and there have been very limited studies on the biology and distribution of this species. The presence of *Pachnodus fregatensis* was first reported in 1972 (as *Pachnodus ornatus*) (Lionnet 1972) although it was not described as an endemic species until 1980, based on specimens collected in 1972 on banana trees along the Rivière Bambou (Van Mol & Coppois 1980).

During July 1995, brown rats *Rattus norvegicus* were unintentionally introduced and rapidly became established on the island. They are a highly invasive species and known to pose a threat to certain endemic animals (Thorsen & Shorten 1997). In view of this, in 1996 a rescue collection of Enid snails, along with Giant Tenebrionid

Beetle *Polposipus herculeanus*, Giant Millipede *Seychelleptus seychellarum* and Giant Scorpion *Chiromachus ochropus* was sent to the Zoological Society of London as part of an ex-situ captive breeding programme (Lucking & Lucking 1997; Gerlach 1999) in order to safeguard the survival of these vulnerable species of Frégate Island.

In 2000, Gerlach and Florens had raised concerns about the potential impact of rodent eradication on the invertebrates of Frégate and had shown that *Pachnodus* snails are highly vulnerable to poisoning. Rats had been reported on Frégate from at least the 1960's (Dawson 1965), although they appear to have been eliminated from at least 1985 - 1995 (Gerlach 2005).

In 2005, Gerlach revealed that between 1999 and 2001, the population of Frégate Enid snails had declined by a significant 87% and he estimated the population to be approximately 7700 individuals. The result of this decline seems to be the broadcast use of the anti-coagulant Brodifacoum in the successful eradication of brown rats from the island in 2001 (Merton *et al.* 2001).

Being an important component of a healthy functioning ecosystem, snails are considered potential bio-indicators of the impact on climate change (Gerlach 2010). Despite their importance, these molluscs face a number of potential threats on Frégate, including habitat alteration, direct poisoning used in eradication of introduced species (Gerlach 2006), as well as changing weather patterns and possible threats from introduced species. Three, possibly four, snail species have already become extinct in the Seychelles, along with extinctions of at least eight plant species, three tortoise species, one mammal species, one crocodile species, seven bird species and likely many invertebrate species (Nature Seychelles, S.a.). *Conturbatia crenata*, a species described by Gerlach in 2001 from a single specimen found on Frégate in 1999 is likely the fourth snail species to become extinct (Gerlach 2005), even before any data has been collected on its biology and distribution.

In the decade since 2001, no thorough population assessments have been undertaken to determine the population trend of Enid snails and it was unknown whether the population had recovered since the eradication of rats. The purpose of this study was to establish whether there has been a recovery of the population and if so, to what extent. The vegetation on Frégate has also changed during this period and this study served to determine the distribution of the species. With limited historical data on *P. fregatensis* and with small, isolated populations being vulnerable to extinction, optimal conservation decisions need to be made to ensure the continued survival of this species. To do so effectively, up to date information is necessary and population trends are essential.

Study area

Frégate is a privately owned island of 219 hectares, forming part of the inner granitic group of the Seychelles archipelago. The island lies at 04°35′19′′S and 55°56′55′′E, with its highest point being Mont Signal situated 125 m above sea level. Deposits on the plateau are associated with guano; forming phosphate cemented sandstones and phosphatised granite. The low-lying areas were swampy in the past and characterized by sediments of fine clay and quartz (Braithwaite 1984). These swampy areas have been replaced by agricultural fields, manicured lawns and a marina development. Frégate, as the seventh largest granitic island, was probably isolated from the rest of the Seychelles islands approximately 12,000 years ago following the break-

up of Gondwanaland (Gerlach 2005).

The vegetation of Frégate has been significantly altered by man's activities and little is known of the island's original vegetation structure (Ferguson & Pearce-Kelly 2005). A description of Frégate in 1787 describes low trees and scrub (Fauvel 1909). Continuous human occupation of the island is thought to have commenced in the early 19th century with a resultant clearing of native vegetation for the establishment of plantations, particularly coconut *Cocos nucifera* (Robertson & Todd 1983). During the early 1900's the island was used for spice and copra production (Merton *et al.* 2001). At present, the vegetation on the island comprises of diminutive patches of native woodland that have either persisted or been replanted, along with exotic species such as cashew *Anacardium occidentale,* banyan *Ficus benghalensis*, cinnamon *Cinnamomum verum* and cocoplum *Chrysobalanus icaco*, amongst others. A large portion of the island was set aside for a vanilla plantation in the early 1900's with sandragon trees *Pterocarpus indicus* being used to support the vines. This area provided habitat for the snails in the past (Gerlach 2005), however these trees were affected by a fungal disease in 2001 that has since destroyed them (Boa & Kirkendall 2004). This area has regenerated naturally and provides potential habitat for the Enid snail and other species.

Methods

Fieldwork was conducted in August 2011 when the snails are active and the probability of underestimation is reduced. The island was stratified into vegetation types based on maps from Gerlach (2005) and Henriette & Rocamora (2009) and updated by Canning (2011). Updated vegetation distribution is based on changes that have occurred as a result of habitat restoration and natural vegetation regeneration. A repeatable pilot study of the entire island determined the presence or absence of snails in each vegetation type.

Surveys were carried out in the mornings between 07:00 and 10:00 before snails retreated into crevices or other hideaways. The vegetation types in which the snails were present were assessed for substrate preference and population distribution. An estimate of the population is based on methodology previously used by Gerlach in 1999 and 2002 to allow for the comparison of results and determination of trends.

A system of random quadrats was used. In each vegetation type surveyed, ten quadrats of 5 x 5m ($25m^2$) were randomly placed and GPS co-ordinates were recorded. The use of randomized quadrats allows the molluscs to be studied regularly without requiring sophisticated marking of location techniques and over-sampling of small areas. Surveyed sample sites were marked using a frame of four steel poles of $25m^2$. In each quadrat a total count of live snails was conducted. Snails were exhaustively searched for by lifting all litter and searching as well as by inspecting the trunks of trees found within the quadrats. The population was estimated by multiplying the estimated mean per square metre, for the surveyed area, by the area over the entire island that is available for the species to occupy. The area available to be occupied by these snails was determined by using Google Earth Pro, version 6.0.3.2197.

All substrates used by the snails were recorded. These substrates were divided into "coconut palm", which consist of live coconut palms, "coconut leaf litter", "soil", "other species" which included *Cinnamomum verum*, *Terminalia catappa*, *Panicum maximum, Alstonia macrophylla, Premna obtusifolia*, *Chrysobalanus icaco*, *Anacardium occidentale* and an agave species. Substrate, described as "other substrate", is terrestrial

and includes rocks, unidentified leaves, branches and coconuts.

Results

Snails were encountered in five vegetation types; these being *Alstonia* dominated mixed exotic woodland, coastal woodland, exotic scrub planted with natives, coconut plantation and mixed exotic scrub (Fig. 1). These sites ranged from 13m to 105m above sea level. These vegetation types differ greatly in terms of species composition, vegetation densities and microhabitat availability. The results of these differences are reflected in the distribution and densities of snails with the snails found in habitats dominated by exotic species. 124 individuals were enumerated from the 50 surveyed quadrats.

*P. fregatensis*is unevenly distributed on the island and is found in densities varying between 0.268 /m² in *Alstonia* dominated mixed exotic woodland, 0.032 /m² in mixed exotic woodland, 0.016 /m² in coastal woodland,0.084 /m² in exotic scrub planted with natives and 0.096 /m² in coconut plantation with the mean density across habitat types being 0.0992/m² (Table 1).

The area available across all vegetation types in which this species is found was determined to be 644,054 m². Using the mean density multiplied by the area available to

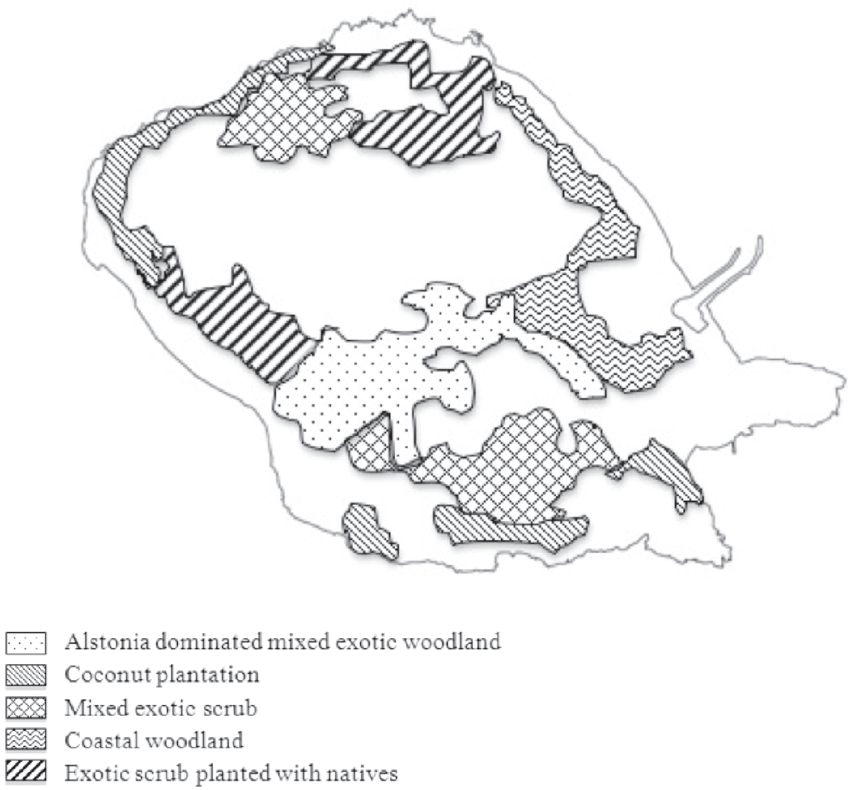

Figure 1. Spatial distribution of *Pachnodus fregatensis* on Frégate Island

these snails, the population was estimated at 63,890±11,361 individuals. These results indicate a significant increase from the results of the 2002 assessment (Table 2).

One way ANOVA determined that the distribution of snails between habitats is statistically significant ($F = 2.9713$, $P < 0.05$) with the majority of snails (54%) being found in *Alstonia* dominated mixed exotic woodland, despite this vegetation type accounting for only 21.5% of available habitat. Coastal woodland accounted for the lowest percentage of snails with only 3.2% of observed snails occupying this vegetation type. Exotic scrub accounted for 17%, coconut plantation for 19.3% and mixed exotic scrub for 6.4%.

The substrates on which snails are found in each vegetation types are determined largely by the species composition of the vegetation in that particular habitat. Non-native species dominate all habitat types in which snails are found with the presence of *C. nucifera* appearing to be advantageous to the species. In all habitats, living *C. nucifera* and their decaying leaves were utilized as a substrate. The leaves form dense carpets on the ground and moisture retention amongst these leaves is high, providing a suitable microhabitat for snails. In determining the substrate usage by the snails, a Chi² test indicated a significant association with certain substrate types. $X^2 = 50.93$, $P<0.01$ at 16df indicating a statistically significant difference between substrates (Table 3).

Discussion

Pimm (1988) notes that the problem of extinction should be seen primarily as the problem of endemism and that endemic species need to receive priority in protection. As an endemic species, the extinction risk for Enid snails is high and with changing weather patterns and possible future changes in land use this species still faces threats to its survival. Habitat alteration is considered the single biggest threat to species worldwide (Soule 1991) and the anthropogenically induced fragmentation and transformation of Frégate's natural vegetation has undoubtedly had an impact on the

Table 1. Density and numbers of *Pachnodus fregatensis* per vegetation types in which they were found

Vegetation type	Area (m²)	No. Snails	Density (m^{-2})
Alstonia dominated mixed exotic woodland	138,973	67	0.268
Coastal woodland	100,519	4	0.016
Exotic scrub planted with natives	132,092	21	0.084
Coconut plantation	111,753	24	0.096
Mixed exotic scrub	160,717	8	0.032
TOTAL	**644,054**	**124**	

Table 2. Population trend of *Pachnodus fregatensis*

1999	2002	2011
57,910±5,407	7,730±880	63,890±11,361

Table 3. Observed and expected frequencies for substrate use by *Pachnodus fregatensis* on Frégate Island in each vegetation type generated by a Chi-square test (n =124, P≤ 0.01).

	***Alstonia* dominated**	**Coastal woodland**	**Exotic scrub planted with natives**	**Coconut plantation**	**Mixed exotic scrub**	**Total**
Observed:						
Coconut palm	10	3	6	14	7	40
Coconut leaf-litter	26	0	12	10	0	48
Soil substrate	11	1	1	0	0	13
Other species	6	0	2	0	1	9
Other substrate	14	0	0	0	0	14
Total	*67*	*4*	*21*	*24*	*8*	*124*
Expected:						
Coconut palm	21.6	1.29	6.7	7.74	2.58	
Coconut leaf-litter	25.94	1.55	8.1	9.2	3.1	
Soil substrate	7.02	0.42	2.2	2.52	0.84	
Other species	4.86	0.29	1.52	1.74	0.58	
Other substrate	7.56	0.45	2.37	2.71	0.9	

distribution and abundance of its native fauna. *P. fregatensis* occurs in these disturbed habitats, although with limited historical data it is difficult to conclude whether or not the population size is anywhere near pre-habitation by man and any further fragmentation may pose a very real threat to the continued survival of the Enid snail.

The distribution of snails is clumped in suitable habitats with individuals being isolated from each other due to their low powers of dispersal. Historically snails have been found along the Rivière Bambou and the agricultural plateau within coastal and mixed woodland as well as in exotic *Pterocarpus* woodland (Gerlach 2005). *Pterocarpus* woodland has been replaced by mostly native species that have naturally regenerated. No snails were found in this habitat type, probably due to this regenerated habitat type being less than a decade old and with these snails having poor powers of dispersal, they are likely to disperse into this area over time. The thick leaf litter that is found in this habitat should provide a suitable microclimate for the species.

Dispersal of Enid snails into previously unrecorded areas around the hotel and villas was first reported by Pearce during a field trip by the Zoological Society of London in March 2011 and corroborated in the latest assessment. Significant amounts of both native species and non-native species have been planted in this area since the development of a hotel and further habitat restoration and the creation of suitable corridors on the island would facilitate the dispersal of this species into new and suitable habitats on the island.

The eradication of rats from Frégate Island is justifiably considered a success in terms of conservation intervention. This action was a factor in the survival of the Seychelles Magpie Robin *Copsychus sechellarum* as well as contributing to the welfare of other native species. Despite the impact this intervention had on the snails, the significant increase in the size of the population between 2002 and 2011 indicates a strong resilience and ability to recover rapidly from a depleted population size; provided suitable habitat is available and external risk factors are excluded or reduced. The increase in the population can be attributed to the cessation of the use of poison in snail habitat since the eradication of the rats as well as the change in vegetation structure for both habitat restoration and ornamental purposes.

With limited historical records of the vegetation of Frégate, it is difficult to accurately determine the natural distribution and abundance of Enid snails in particular habitats and the lack of regular monitoring of the species provides only limited data on population trends. However, now that a baseline has been determined both post and prior to conservation interventions, it is important to maintain a monitoring protocol for the Enid snail. The conservation of this species and others on the island lies in the conservation and correct management of the habitat.

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Red Listing reveals the true state of biodiversity: a comprehensive assessment of Seychelles biodiversity

Justin Gerlach

Nature Protection Trust of Seychelles, PO Box 207, Mahe, SEYCHELLES
133 Cherry Hinton Road, Cambridge CB1 7BX, U.K.
[*jstgerlach@aol.com*]

Abstract: The status of all terrestrial and freshwater multicellular organisms in the Seychelles islands is assessed based on IUCN Red List criteria. This covered 4,841 soecues if fungi, lichens, plants and animals. 34% of species were assessed as threated. Threat levels for most groups were around 30%, with exceptionally high levles of threats in molluscs (61%) and vertebrates (62%). Lower threat levels in other groups are partly due to higher levels of uncertainty in some groups, with Data Deficiency being over 50% in fungi, Bryophyta, Nematoda and Rotifera, and 38% in Arthropoda. Endemic species show higher levels of threat than indigenous species in almost all taxa, due to endemics being largely narrow range species and indigenous species including many that are widespread recent colonists. Species restricted to the coral islands show exceptionally high threat levels as a result of beign limited to low lying islands threatened by sea level rise. The main threat factors are identified and show a change from largely historical threats such as hunting and deforestation, to habitat degradation resulting from the impacts of invasive species and climate change. 23 species are considered to be Extinct, with a further 232 species possible extinctions. The causes of these extinctions are discussed.

The IUCN Red List has become the standard tool for evaluating the threatened status of organisms, the assessment criteria enabling individual assessments, comparisons between taxa, areas and time periods (Rodrigues *et al.* 2006). However, comprehensive assessments only cover a small proportion of the world's biodiversity, such as birds, mammals, amphibians, cycads and corals. Large scale, but still partial assessments have been carried out on selected freshwater taxa and random samples of other groups have been assessed. This still makes comparison between taxa difficult, particularly for the majority of the poorly known invertebrate taxa (Gerlach *et al.* 2012). Regional or national assessments are similarly limited, with most such assessments covering only a small proportion of the biota, usually easily recorded groups such as vertebrates, some plant groups and a small number of the larger invertebrates. The scope of such assessments needs to be expanded in order to make the Red List a fully functional tool in monitoring biodiversity conservation trends, both at local and global scales.

The Indian Ocean Biodiversity Assessment 2000-2005 (IOBA) was undertaken by Nature Protection Trust of Seychelles to assess the composition and status of all aspects of biodiversity in the Seychelles islands. This resulted in a series of monographs on the fauna of the islands (Gerlach 2007a, 2007b, 2008, 2009, 2011, 2013, Gerlach & Haas 208, Gerlach & Matyot 2006, Gerlach & Marusik 2010) which include Red List assessments for all native animal species. Assessments of the endemic Mollusca,

Vertebrata and Orthopteroidea have been included on the IUCN Red List, the other taxa are in the process of inclusion on the list. In addition to these assessments compiled by the author, all endemic granitic Seychelles vascular plants and pteridophytes are on the IUCN Red List (except for *Impatiens gordonii*). The only multicellular taxa not to have been assessed are the Bryophyta, Fungi and lichens, and the plants of the coral islands. Here I present a summary of the Red List status of all Seychelles species, including a provision assessment of the Bryophyta, Fungi, lichens and non-endemic plants, with an analysis of the status of the biodiversity and the main threat factors.

Assessments

IUCN Red List criteria (IUCN 2001) have been applied to all native taxa (indigenous and endemic). Taxa believed to be introduced have not been assessed. These assessments are based on historical collections and data collected during the IOBA on most of the 115 islands of the Seychelles group (Gerlach 2003). Quantitative data were collected in all main habitats on each island (methods are fully described in Gerlach 2003). These data allowed distributions and habitat associations to be determined for each species, and in some cases population sizes could be estimated. Historical data comprised distribution data from historical collections, comprising island records only (1892) or more precise localities within islands (1894, 1905-9, 1954-6, 1972 and 1984), these were compiled from literature or collection labels. These data allow distributions to be compared. They give no data on population sizes but may provide an indication of relative abundance, for example, where a species was collected in large numbers (at least 50 specimens) in 1908 but has only been found as isolated individuals subsequently a population decline can be inferred (but not quantified).

In assessing the Red List status of a species different criteria were useful for different types of organism, these are summarised in Table 1. Taxa were considered Extinct where extensive searches have been carried out in the known range and similar habitats and the species has not be located for 50 years. A shorter time period is used for species that have been monitored closely and decline has been observed, followed by a failure to find any surviving individuals despite intensive searching. Taxa not recorded for over 50 years but not subject to careful searches, or from taxonomically confused groups were considered Data Deficient.

Table 1. Red List criteria used in assessing different taxa

Criterion	Outline	Application
A	Population decline	vertebrates, molluscs, some insects and plants
B	Range/habitat decline	all taxa
C	Population restricted and declining	vertebrates
D	Population size	vertebrates, some molluscs and plants
E	Modelled extinction risk	vertebrates

Threat levels

34% of the 4,841 native species were assessed as threatened (Table 2). Of the multicellular kingdoms (Fig. 1) threat levels are highest for animals (32%) and lowest for fungi (18%), but this latter value is unreliable due to the high proportion of Data Deficient species (more than 50%). Plants have an overall threat level of 30%.

Of the plants, the bryophytes show the lowest level of threat (22%) due to the high proportion of Data Deficient species in this group; its true threat level is probably closer to that of the other plant groups, both of which have similar threat levels (37% for pteridophytes and 33% for angiosperms).

Total threat rate for animals is 36% and particularly high threat levels are recorded for Mollusca and Vertebrata (excluding the phyla with very small numbers of species). The moderately high level of threat for animals as a whole is the result of the data being skewed by the arthropods which make up 92% of Seychelles animal species and 85% of the arthropods are insects (Hexapoda). Within the arthropods Crustacea show the highest level of threat, and Myriapoda the lowest.

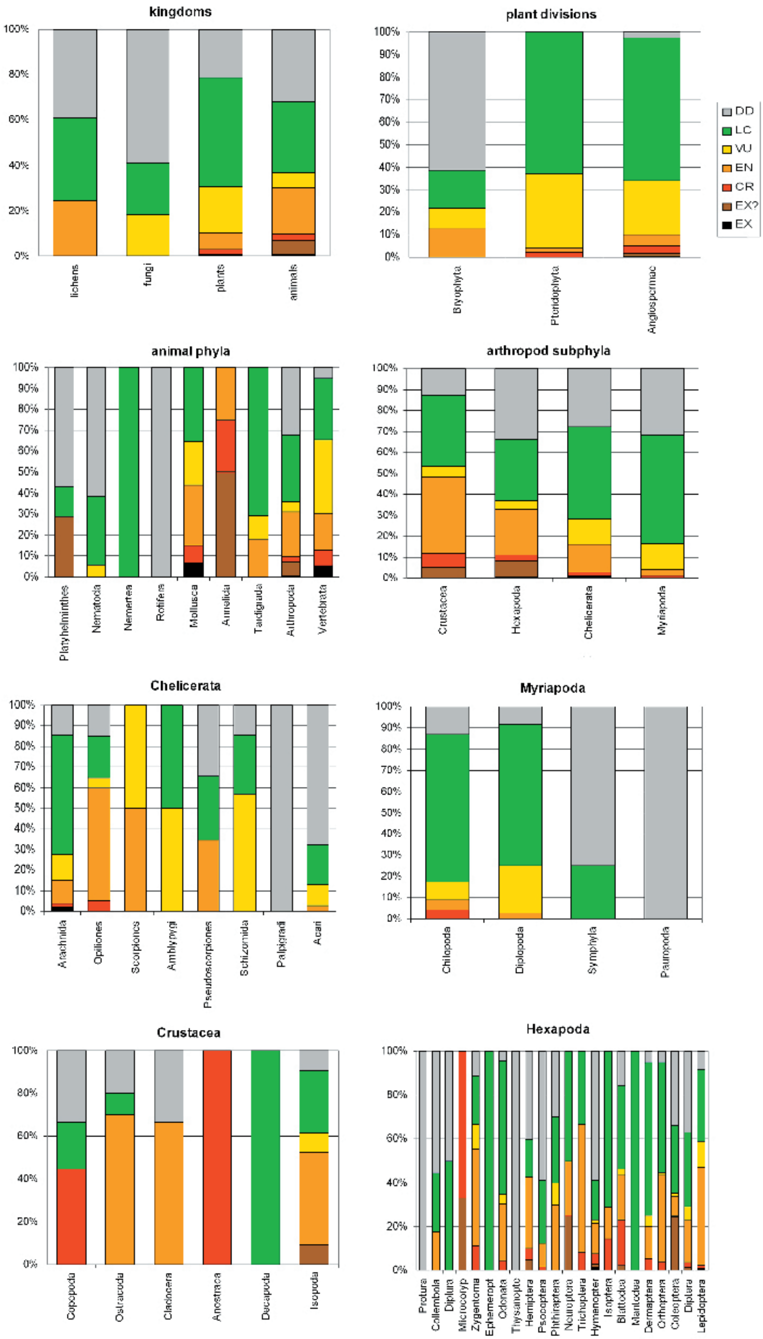
Global comparisons

It is difficult to determine whether or not this level of threat is unusually high as there are few comprehensive assessments available for comparison. At present the Red List is dominated by non-comprehensive assessments and the raw figures give misleading results, for example 63% of plants and 50% of fungi on the global Red List are threatened, as few non-threatened taxa have been assessed. The comprehensive assessments show a wide range of threat levels, for plants they vary from 30% (conifers) to 63% (cycads). Non-marine vertebrates range from 41% in amphibians, to 25% in mammals and only 13% in birds. For non-marine invertebrates only freshwater crabs

Table 2. Summary of assessment, threatened categories are EX?, CR, EN, VU

Taxon	EX	threatened	NT	LC	DD	total	% threatened
Lichens	0	99	0	148	158	405	24
Fungi	0	8	0	10	26	44	18
Bryophyta	0	53	0	40	148	241	22
Pteridophyta	0	36	0	61	0	97	37
Angiospermae	2	135	8	239	10	394	35
Platyhelminthes	0	2	0	1	4	7	(29)
Nemertea	0	0	0	1	0	1	(0)
Nematoda	0	3	0	17	32	52	6
Annelida	0	4	0	0	0	4	(100)
Mollusca	4	43	1	26	0	74	61
Rotifera	0	0	0	0	35	35	(0)
Tardigrada	0	4	0	24	0	34	29
Arthropoda	10	1305	1	1048	1277	3645	36
Vertebrata	7	66	3	32	6	114	62

Fig. 1. Comparison of threat levels faced by major multicellular taxa in Seychelles



have been assessed comprehensively at a global level. At a regional level (reviewed in Gerlach *et al.* 2012) European assessments are the most complete; these tend to show lower levels of threat than recorded here: in Scandinavia invertebrates have low threat levels – annelids <1-4% (varying in different country assessments), molluscs 7-13%, chelicerates 3-12%, myriapods 4-8% and insects 9-10%. Assessments from Germany and Poland have high threat levels, but these cannot be used comparatively as they are not fully comprehensive or use slightly different criteria.

The available comparative data suggest that Seychelles has a high level of threat for most major taxa; that ratio between the Seychelles threat level and that from comparative sites gives molluscs a 4.9 times higher threat level, chelicerates 2.3, myriapods 2, insects 3.7 and vertebrates at least 1.5. The comparative data are largely drawn from continental sites (most of the species in the global assessments and all of the comprehensive national assessments) and it is probable that at least a part of the elevated threat level of the Seychelles biota reflects island vulnerability.

The assessments are further divided into indigenous and endemic taxa, granitic and coralline islands and terrestrial and freshwater (Fig. 2).

Endemics and natives

For animals 43% of endemic species are threatened but only 26% of indigenous species. Endemic vetebrates are nearly twice as threatened as indigenous species (84% compared to 44%), slightly lower differences are found in molluscs (78% to 44%) and arthropods (42% to 27%). Within the arthropods endemic myriapods are more than five times as threatened as indigenous species (27% compared to 5%), crustaceans are more than twice as threatened (69% compared to 31%), chelicerates nearly twice as much (34% compared to 18%). Insects have the lowest level of difference with 43% compared to 29%.

Geographical system

All taxonomic groups show higher threat levels in the atolls than the granitics (mollusucs - 100% of endemic species and 40% of indigenous compared to 74 and 13%; arthropods – 80 and 53% compared to 35 and 35%; vertebrates 91 and 51% compared to 81 and 18%). Within the arthropods very high levels of threat in the atolls is found in the Crustacea (100 and 62% compared to 63 and 31%), high levels in insects (81 and 54% compared to 35 and 36%) and chelicerates (75 and 38% compared to 30 and 31%). The one oddity are the myriapods which are very scarce in the atolls, lacking endemic atolls species, they have 33% threatened indigenous species in the atolls, which is almost the same as in the granitics which have 27% threatened endemics and 38% threatened indigenous species.

Atoll species are all threatened by climate change, with sea-level rise being project to cause significant loss and degradation of habitat in these low-lying islands. Invasion is relatively low in the atolls (at least compared to the granitics) and this is only a minor, contributory threat to most species. Threats in the granitics (discussed futher below) are more diverse, and invasion is the main active threat.

Fig. 2. Comparison of threat levels faced by endemic and indigenous species systems of the proportion of species in each RL category

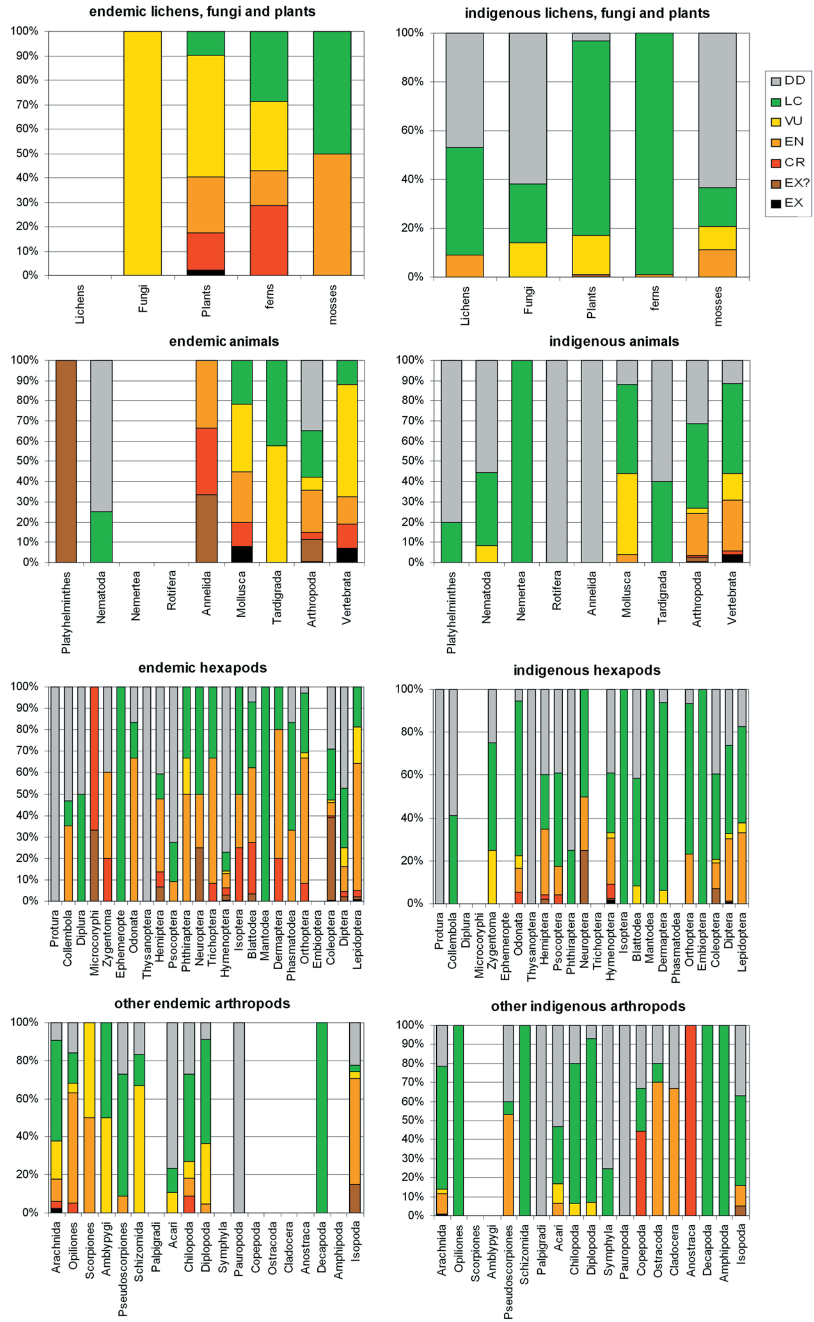
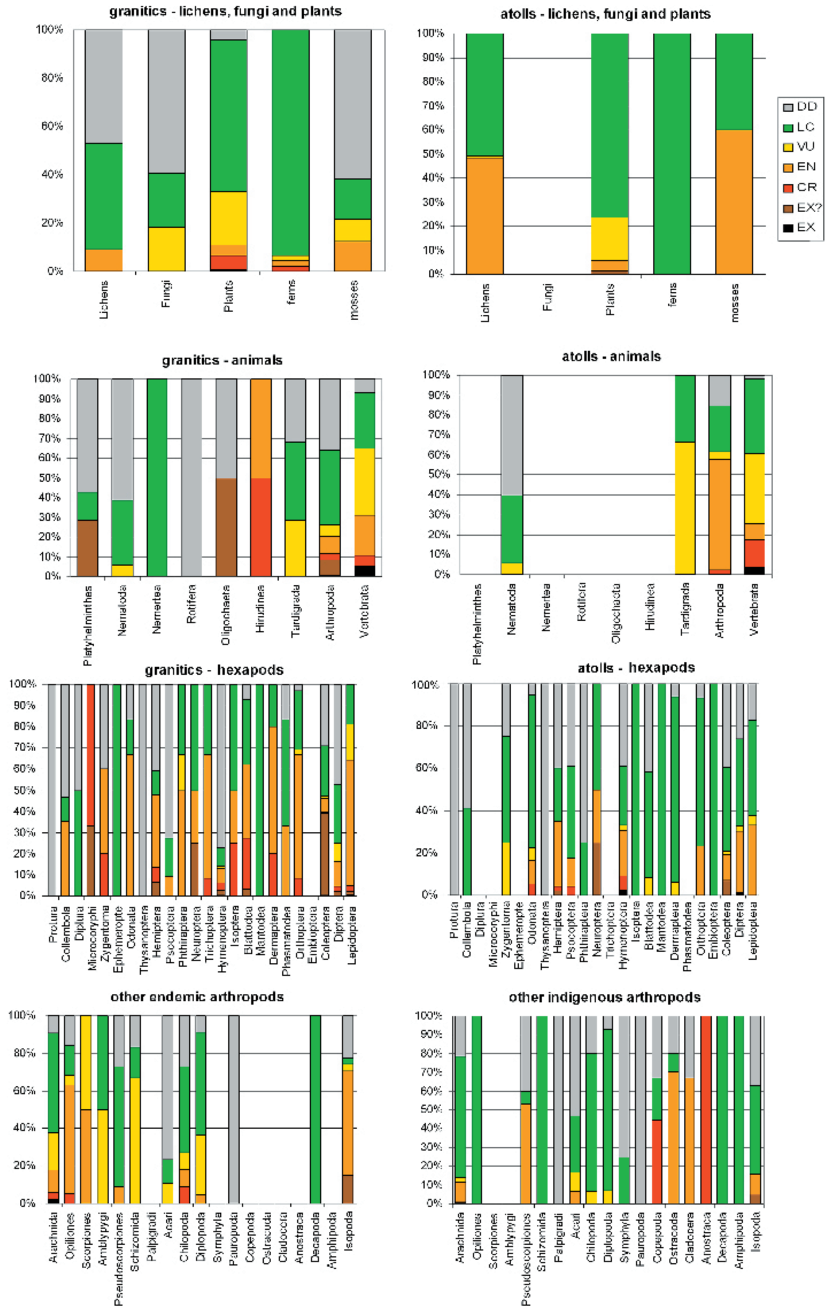


Fig. 3. Comparison between granitic and coralline islands of the proportion of species in each RL category



Terrestrial and freshwater

Differences between terrestrial and freshwater systems are minor, with animals having overall threat levels of 30% on land and 37% in freshwater. There are very few groups that have significant numbers of species in both systems; taxa with more than 10 species in each system are the vertebrates, which are 63% threatened on land and 33% in freshwater and several insect orders. The bugs (Hemiptera) are 42% threatened on land and 52% in freshwater, beetles (Coleoptera) 28% on land and 51% in water, flies (Diptera) 21% on land and 37% in water. This is notable in that vertebrates are more threatened on land than in water whereas all the insect groups are more at risk in freshwater, this is due to the freshwater vertebrates being mainly widespread Indo-Pacific estuarine fish or Data Deficient species. Data Deficiency in freshwater vertebrates is 50% compared to only 6% on land. Exclusively aquatic groups are also highly threatened (excluding the Data Deficient rotifers and very low diversity groups) – freshwater crustaceans having threat levels of 44-70% in the most diverse groups (Copepdoa and Ostracoda), 39% in Odonata and 67% in Trichoptera.

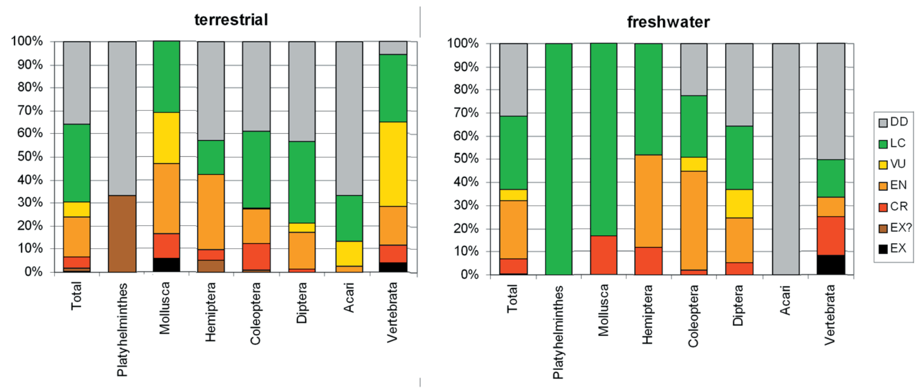
The general higher level of threat in freshwater than on land is due to the restricted nature of this system in Seychelles. This means that all populations are small and often very isolated, and as such are inherently vulnerable to extinction. This natural vulnerability is exacerbated by habitat degradation caused by invasive species in or near water courses, and by climate change affecting stream-flow.

Taxonomic patterns

Lichens

Lichen data is of reasonable quality for the larger islands (Mahé and Silhouette mainly, with some data from Praslin but very little from La Digue). Smaller islands are probably under-collected but diversity is extremely low on those islands that have been sampled. These have moderate levels of threat (24%) and Data Deficiency (39%).

Fig. 4. Comparison between freshwater and terrestrial systems of the proportion of species in each RL category



Fungi

Fungi are very poorly known in Seychelles and the 44 free-living species identified are clearly only a small proportion of the true level of diversity. Accordingly it is not surprising that Data Deficiency is very high at 59%. Identified threat level is 18% but this cannot be taken to be reliable.

Plants

Overall threat levels for plants are 31%, with a moderate level of Data Deficiency (22%). Most of the uncertainty for plants arises from the bryophytes where 61% of species are Data Deficient. This is due to a paucity of published data on this group, recent extensive collections have yet to be identified, when that has been completed a more accurate picture of the status of byrophytes, and plants in general, will emerge. For the pteriodphytes and angiosperms Data Deficient species make up 0 and 3% respectively, and in these groups threat levels stand at 35 and 37%.

Animals

Animals overall are 36% threatened with 32% Data Deficiency, both of which vary widely with different animal phyla. Data Deficiency is particularly high in the Rotifera (100%), Nematoda (62%) and Platyhelminthes (57%). Arthropods have a figure of 32%, but it is low for vertebrates (6%) and all species of other taxa have adequate data for assessment. Excluding the taxa with more than 50% Data Deficiency threat levels are highest in Annelida (100% but only four native species), followed Mollusc and Vertebrata (both 64%). Of the reasonably well assessed taxa Arthropoda have the lowest level of threat (36%). Within the arthropods crustaceans and chelicerates are reasonably well known (13 and 28% Data Deficient respectively), with poorer data in myriapods and insects (32 and 34% Data Deficient). Threat levels are highest in the crustaceans (53%) and insects (37%) followed by chelicerates (28%) and lowest in myriapods (16%).

Extinction (Fig. 5)

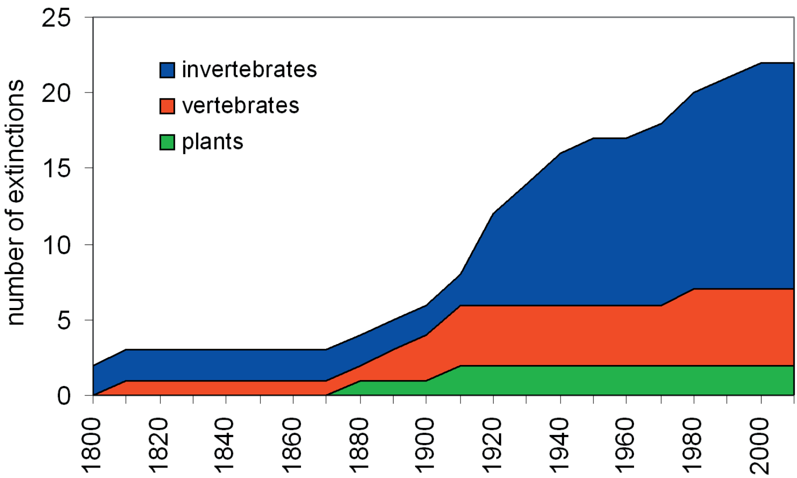
There are no historical data (i.e. pre 1900) with which to identify any extinct lichens, fungi or bryophytes. Although 19th century collections of ferns exist all are apparently extant. Two endemic species of angiosperms are Extinct: *Oeceoclades seychellarum* and *Vernonia seychellarum* were last recorded in 1902 and 1874 respectively; and a small number of indigenous species may have disappeared from Aldabra. These latter species were all isolated records (e.g. *Carissa spinarum*, present in the granitics but restricted to a single record from Aldabra) which may have been naturally rare, becoming extinct through stochastic loss, or may have been affected by climate change or by introduced predators. In the absence of any useful data the causes of extinction can only be speculative.

Recorded animal extinctions comprise 7 vertebrates (one terrapin, five birds and one crocodile) and 14 invertebrates. The vertebrates have been lost through hunting (*Psittacula wardi* [around 1900], *Pelecanus rufescens* [around 1910], *Papasula abbotti* [around 1915], *Crocodilus porosus* [around 1800]), habitat loss and predation (*Zosterops*

semiflava [around 1900]), and unknown causes (*Pelusios seychellensis* [around 1900], *Nesillas aldabranus* [about 1984]). These all date from at least 97 years ago except for the Aldabra warbler which disappeared in the early 1980s. The invertebrates comprise 4 snails and 10 arthropods. The snails were lost to early habitat loss (2 species in the early 1800s: *Pachnodus curiosus, P. ladiguensis*) and recent climate change (*P. velutinus* [1994]*, Rhachistia aldabrae* [1988]*, Glabrennea silhouettensis* [2010]). The arthropods are 4 Hymenoptera, 1 Coleoptera, 1 Lepidoptera and 3 Arachnida that disappeared sometime after 1909, probably due to ecological changes resulting largely from invasive species impacts. In addition one species of butterfly (*Phalanta phorbata*) became extinct around 1953, the cause of this is not known. On Aldabra changes in plant community composition since 1976 seems to have resulted in the extinction of the endemic butterfly *Acraea terpsichore legrandi* and a decline in the abundance of *A. ranavalona*.

In addition to these probable extinctions a large number of species have been categorised as 'Critically Endangered – possibly extinct': 2 Platyhelminthes, 2 Oligochaeta, 4 Isopoda, 1 Microcoryphia, 17 Hemiptera, 4 Neuroptera, 5 Hymenoptera, 1 Blattodea, 185 Coleoptera, 8 Diptera, 2 Lepidoptera, 1 Arachnida. Of these, the cockroach is *Margattodea amoena* which was endemic to Desroches atoll and is almost certainly extinct following extensive habitat loss on the island. Lepidoptera placed in this category are both very little known species – *Nephele leighi* from the granitic islands last recorded in 1969, and *Bataconema coquereli aldabrensis* from Aldabra in 1895. Several species were damp forest associated species which may have disappeared due to habitat change caused by invasive species, direct competition with invasives, or unidentified factors (flatworms, earthworms, the microcryphian species). The hemipterans were mainly phytophagous species, the majority forest planthoppers, with a smaller number of predatory species such as reduviids. The probably extinct Hymenoptera were all predatory (Ampulicidae, Crabronidae) or parasites of hemipterans (Encyrtidae).

Fig. 5. Increase in number of recorded extinctions since 1800



The Coleoptera were predominantly forest weevils (Curculionidae) and leaf-beetles (Chrysomelidae). In addition smaller numbers of darkling beetles (Tenebrionidae), scarabs associated with palms (Scarabaeidae) and a longhorn beetle (Cerambycidae) may have been lost as a result of close associations with particular plant species. A small number of possibly extinct species were predators in the Carabidae, Cleridae, Coccinellidae, Cleridae and Histeridae, with the exception of the carabid species these would all have been predators on vegetation and may have been affected by changes in prey communities. The flies were forest predators (Asilidae: *Heligmonevra insularis, Laphria cyaneogaster*; Muscidae: *Coenosia extincta*) or parasitoids of planthopper bugs (Pipunculidae: *Microcephalus depauperatus, Clistoabdominalis nitidifrons, Eucorylas semiopacus, Tomosarella sylvaticoides*) with the exception of the little known tephritid fruit fly *Taomyia ocellata*. Thus the possibly extinct invertebrates cover leaf-litter and soil and foliage inhabiting species from widely differing taxonomic groups, united only in being forest associated (as is most of the invertebrate fauna).

Critically Endangered species make up only 3% of Seychelles animals as a whole and are found in a wide range of taxa, with particularly high levels in the Annelida (25%), Copepoda (44%), Anostraca (100%), Microcoryphia (40%), Zygentoma (20%), Isoptera (14%) and Blattodea (21%). These figures are misleading as all except the Blattodea are very species poor (fewer than 10 species), the Copepoda and Anostraca are unusual in being largely restricted to freshwater pools on Aldabra, a very restricted and threatened habitat, but the species themselves are widespread outside of Seychelles. The figures for Blattodea are notable however; these are largely high forest species threatened by climate change causing degradation to their highly restricted habitats.

Threat factors

Five threat factors have been identified in the Red List assessments for Seychelles: hunting, predation, habitat loss, habitat degradation caused by invasive species and habitat degradation caused by climate change.

Hunting is a historical cause of extinction and direct consumption of the surviving species is very limited (although still occurring with the fruit bat *Pteropus seychellensis*, various seabirds and the tree *Deckenia nobilis*). Predation is similarly historical threat, although it may prevent recolonisation of historic ranges for some species. Direct loss of habitat through clearance for agriculture and development has been significant in the past and the urban development aspect is recurring as a threat to lowland species, although affecting only a small percentage of species. Habitat change as a result of invasives has been identified as a contributory factor to almost all threatened Seychelles species. Habitat change as a result of climate change is a significant threat to the Critically Endangered high forest species and to those restricted to low-lying islands where sea level rise will be a major issue. Comparisons of the threats affecting granitic and coral island species are shown in Fig. 6, highlighting the over-riding nature of sea-level (climate change) rise in the coral islands and the more diverse nature of threats in the granitic islands. Invasive species are the predominant threats in the granitic islands although this is now combined with climate change.

Assessing historical changes in threats is not practical for most taxa due to a

paucity of early data. Vertebrates have relative good data, with locality records dating from the mid 19th century which enable early threatened status and threat factors to be identified. Molluscs lack good locality records until 1894 but a good subfossil record allows historical distributions to be reconstructed. These two groups provide indications of how threat factors have changed over the past 200 years (Fig. 7).

Discussion

The analysis of the status of the biodiversity of Seychelles presented here uses the IUCN Red List criteria to provide a comprehensive assessment of the state of biodiversity and to identify the main threatening factors across all species. This shows that habitat factors are the most important influences of extinction risk for the vast majority of species, with invasive species and climate change being the main causes of habitat deterioration.

Fig. 6. Threat factors identified in the granitic and coral islands

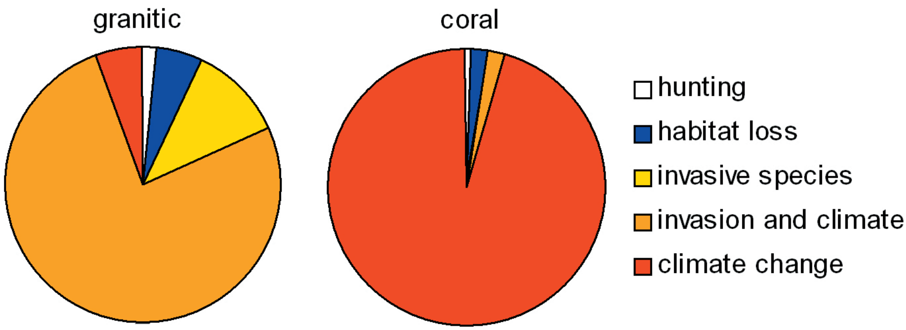
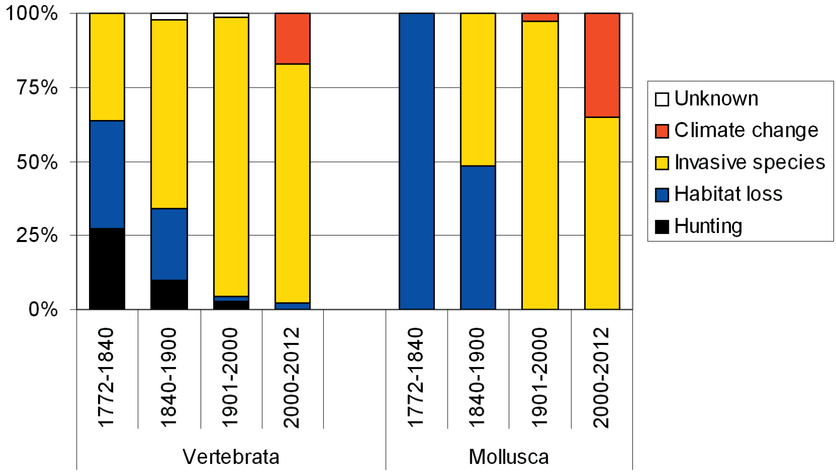


Fig. 7. Threat changes over time in groups with useable early records in the granitic islands.



At present 34% of species in Seychelles are at risk of extinction, with at least 23 species having been driven to extinction already. True levels of exinction are probably considerably higher, with 232 species being identified as ‘Critically Endangered – possibly extinct’. There would also have been an unknown number of species having been lost before scientific collections started, for example, of the molluscs two of the extinct species are known only from subfossil shells. This level of threat is indicative of a true ‘biodiversity crisis’ and demonstrates the need for urgent action to reduce the impacts of invasive species and climate change.

Acknowledgements

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Changes in non-marine mollusc populations in the Seychelles islands 1986-2012

Justin Gerlach
133 Cherry Hinton Road, Cambridge CB1 7BX, U.K. [jstgerlach@aol.com]

Abstract: Population changes in Seychelles terrestrial molluscs were investigated using monitoring data from 1986-2012 at 18 sites on the islands of Mahé, Praslin and Silhouette. Species with significant changes in populations could be categorised as fluctuating (populations increasing or decreasing at different times and in different localities), decreasing (significant declines in most occupied sites) or increasing (significant increases in most sites). Fluctuating species included the helicinid *Pleuropoma theobaldiana* and the streptaxids *Edentulina dussumieri, Seychellaxis souleyetianus* and *Steorestele nevilli*. Two species were identified as increasing: *Subulina striatella* and *Leptichnoides verdcourti*, both invasive species currently expanding their ranges. five species are in decline in some sites but not others: *Augustula braueri, Imperturbatia constans, Silhouttia silhouettensis, Priodiscus serratus* and *Pachnouds ornatus*. 10 species are in decline: *Moominia willii, Edentulina moreleti, Glabrennea gardineri, G. silhouettensis, Nesokaliella minuta, Pachnods velutinus, P. kantilali, P. nigerxvelutinus, P. oxoniensis* and *Stylodonta unidentata*. Declines were attributed to habitat deterioration (*S. unidentata*), climate change (*M. willii, E. moreleti, G. silhouettensis, P. velutinus, P. nigerxvelutinus, P. oxoniensis*) or a combination of the two factors (*Augustula braueri, G. gardineri, N. minuta* and *P. kantilali*). Climate change takes the form of changes in rainfall patterns, most significantly a decrease in rainfall in the first quarter of the year. The reduction in rainfall is thought to cause increased mortality of juvenile snails, particularly for arboreal species. This results in the most rapid declines in the highest-altitude and most specialised species. Island snails may be particularly vulnerable to climate change impacts due to their poor dispersal ability and restricted ranges, especially when combined with habitat fragmentation and deterioration due to the spread of invasive plants. Further monitoring of invertebrate populations is needed to determine whether or not snails are particularly vulnerable and how widespread these impacts are.

Populations and ecosystems are thought to be changing in many parts of the world due to factors such as the spread of invasive species, exploitation and climate change. This is resulting in elevated extinction risk and ecosystem instability (Mace *et al.* 2005). Population declines are well established for some well studied vertebrate taxa but such data are scarce for most invertebrates. As a result assessments of threats of invertebrates are limited; 0.5% of terrestrial invertebrates have been assessed for the IUCN Red List (Gerlach *et al*. 2012). These assessments rely on the evidence of habitat degradation as an indication of population decline, sometime supported with range declines. There is a need for comprehensive assessments of the status of a wide range of invertebrate taxa to enable the true status of biodiversity to be determined. Whilst habitat and range changes may provide some indication of status changes population monitoring data are desirable to demonstrate real changes in population status. Such data are very rarely available for invertebrates, with most cases being butterfly populations (e.g. Van Sway *et al.* 2011); only 0.4% of Red Listed invertebrates have been listed

under population size criteria (according to Cardoso *et al.* 2012).

In the Seychelles islands Red List assessments have been undertaken for all non-marine plant and animal taxa (Gerlach 2012). Invertebrate assessments are based on habitat factors and changes in the frequency of collection over the past 150 years. Population monitoring data are not available for invertebrates, with the exception of molluscs. For snails and slugs quantitative population density data have been collected by the author since 1986 on several islands. Analysis of changes in density estimates over the past 36 years enables population changes to be evaluated, providing a more precise assessment of the conservation status of each species.

Methods

Mollusc populations were investigated in numerous sites across the majority of the islands of the Seychelles group between 1986 and 2012. Of these surveys 18 sites on the three largest of the granitic islands were surveyed on 2-10 occasions over these 36 years (Fig. 1). These sites support populations of all of the species recorded in the granitic islands.

<u>Data collection</u>

In each survey site data were collected at 10 randomly placed points. At each point the ground fauna was recorded by collecting a 1x1m square of leaf-litter. Each sample was sifted to remove large debris and record the larger snail species, and then snails extracting by Winkler extraction. The dried litter was finally searched by hand to remove any remaining snails and empty shells. The empty shells were not included in quantitative data but were used to supplement species lists. In addition each point was used as the centre of a 5x5m quadrat in which all trees over 2m height were identified to species and recorded. Each tree was visually inspected to a height of 3m above ground and all snails on the vegetation recorded. Each snail located in ground or vegetation quadrats was identified to species and assigned to categories of juveniles, subadult or adult. Individuals were assigned to the subadult category if they were approximately adult sized but lacked a lip at the mouth edge (usually associated with sexual maturity – pers. obs.). For species that do not normally develop a lip, the subadult category was not used and animals were considered adult if at least 75% of full adult size.

Four species were geographically highly restricted and focussed surveys were designed specifically for these. *Moominia willii, Edentulina moreleti Glabrennea silhouettensis* and *Dupontia levensonia* were only known from discrete habitat areas covering less than 0.5 hectares. In these areas the snails were either found in leaf litter (*G. silhouettensis*) and could be surveyed with the standard methods used for other species or were arboreal species restricted to the axils of the plants *Pandanus hornei* and *Dracaena reflexa*. In the identified ranges of the snails all accessible axils of these two plant species were examined for snails and the number of live snails recorded. In the case of *E. moreleti* snails were assigned to adult, subadult and juvenile categories, but only adults of the other species were located. Studies for these species dated from 1990-2010 for *G. silhouettensis* and 2000-2010 for the other species.

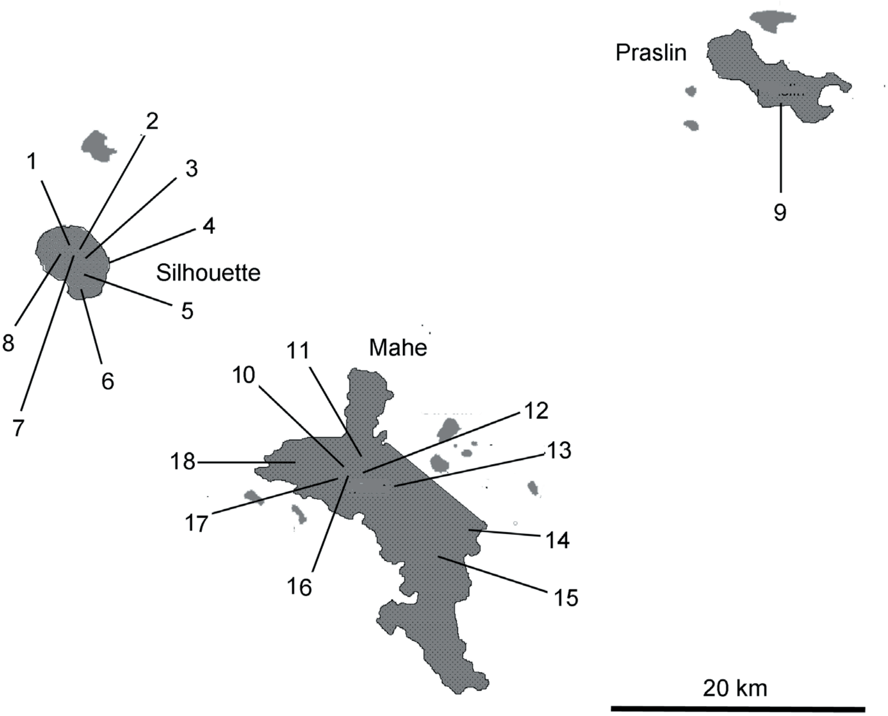
Most surveys were undertaken during the dry season, between June and

August. Some surveys were carried out in November-January and in March. Previous studies have shown that the survey techniques used here are not significantly affected by seasonal variation with no seasonal fluctuations in abundance of adult snails (Gerlach 1995), although reproduction of some species may be affected by climatic factors.

<u>Environmental change</u>

Habitat change was recorded in the same surveys. Plants were counted and identified in each quadrat; in 5x5m quadrats all trees over 2m tall were recorded, in 1m quadrats all plant individuals were counted. Impacts of invasive trees on forest conditions was investigated by recording light intensity levels at the base of 10 trees of each of the 5 most abundant invasive and native tree species in three sites on Silhouette: La Passe, Jardin Marron and Mon Plaisir. Light levels were recorded with a digital light meter (recorded as lux values). All light data were recorded within 10 minutes,

Fig. 1. Map of survey localities. 1 – Anse Mondon valley; 2 – Mon Plaisir; 3 – Jardin Marron; 4 – La Passe; 5 – Gratte Fesse; 6 – south peak; 7 – Pisonia forest; 8 – Mont Dauban; 9 – Praslin National Park; 10 – Congo Rouge; 11 – Trois Freres; 12 – Mission; 13 – Copolia; 14 – Mont Sebert; 15 – La Reserve; 16 – Casse Dent; 17 – Morne Blanc; 18 – Mare aux Cochons



minimising ambient changes in light levels.

Climatic factors were not recorded in the field sites but rainfall and temperature patterns were used from Gerlach (2010) based on data from fixed points (Seychelles Meteorological Office data for Mahé and Praslin islands, Nature Protection Trust of Seychelles data for Silhouette island).

Analysis

An initial analysis of population changes was undertaken by grouping data into three time periods: 1986-1990, 1991-2000 and 2001-2012. Data for each site was treated separately and comparisons made between these time periods for each site using a t-test. For species identified as having significant population changes in these time periods population change was analysed by regression of population against date.

Habitat change was evaluated using t-tests of data from 1986-2000 and 2001-20012. For this analysis plant species were tested individually and a separate analysis was undertaken grouping species into introduced and native species. Climatic change analysis used anomalies from the long term averages to identify periods of unusual rainfall. Annual and monthly data were examined.

The effects of location and of plant species abundance on snail populations was evaluated using a multiple analysis of covariance (MANCOVA) of the abundance of each species of snail, plant species, the total abundance of native and alien plant species and quarterly rainfall averaged over the previous five years. An exploratory analysis found that only one plant species and only first quarter rainfall had a significant impact on any snail species. The analysis was repeated using the abundance of *Cinnamomum verum* and first quarter rainfall. For each snail species data were only included from sites where the species had been recorded, thus avoiding the confounding effects of different geographical distributions.

Results

Snail population changes

Significant changes in species abundance are summarised in Table 1-2 and Fig. 2-4. Four species showed significant population changes but varied in the direction of change and geographical patterns (*Pleuropoma theobaldiana, Edentulina dussumieri, Seychellaxi souleyetianus* and *Stereostele nevilli*). Two species increased in abundance (*Subulina striatella* and *Leptichnoides verdcourti*). 16 species were identified as being in decline (Table 1). All of these are mainly high forest species and 9 species declined at all occupied sites (*Moominia willi, Edentulina moreleti, Glabrennea gardineri, Glabrennea silhouettensis, Nesokaliella minuta, Pachnodus kantilali, Pachnodus nigerxvelutinus, Pachnodus ornatus* and *Pachndous velutinus*). In addition *Nesokaliella intermedia* declined in all sites, but was too scarce for significance testing.

Moominia willii and *Edentulina moreleti* were largely restricted to *Pandanus hornei* axils at Gratte Fesse on Silhouette, with single records from 300 m away at Mon Plaisir. The Gratte Fesse populations were first located in 2000 and declined to very low levels by 2010 (Fig. 4a-b). *Glabrennea gardineri* was recorded at low densities

Table 1. Significant changes in snail populations based on t-tests with 19 degrees of freedom

		1990 vs 2000		2000 vs 210	
		T	P	T	P
Natives	2. Mon Plaisir			2.399	<0.05
	3. Jardin Marron			2.112	<0.05
	7. Pisonia forest			-2.313	<0.05
	8. Mont Dauban			-2.521	<0.05
	9. Praslin NP			2.212	<0.05
	10. Congo Rouge	-2.332	<0.05		
	13. Copolia	-2.451	<0.05		
	14. Mont Sebert			-2.111	<0.05
	16. Casse Dent			2.167	<0.05
	17. Morne Blanc	-2.101	<0.05	-2.327	<0.05
	18. Mare aux Cochons			-2.270	<0.05
Invasives	6. south peak			3.899	<0.001
	18. Mare aux Cochons			-2.541	<0.05
Pleuropoma theobaldiana	7. *Pisonia* forest	2.329	<0.05	-2.099	<0.05
	9. Praslin NP			2.190	<0.05
	10. Congo Rogue	2.131	<0.05		
	13. Copolia	2.365	<0.05	-2.201	<0.05
	15. La Reserve	2.132	<0.05	-2.132	<0.05
	17. Morne Blanc	-2.165	<0.05	-2.221	<0.05
Moominia willi	5. Gratte Fesse			-2.912	<0.01
Subulina striatella	3. Jardin Marron			2.223	<0.05
	5. Gratte Fesse			2.101	<0.05
	6. South peak			2.117	<0.05
	9. Praslin NP			2.491	<0.05
	15. La Reserve			2.511	<0.05
	16. Casse Dent			2.521	<0.05
Augustula braueri	17. Morne Blanc	-2.112	<0.05		
Edentulina dussumieiri	7. Pisonia forest	2.132	<0.05	2.221	<0.05
	15. La Reserve	-2.145	<0.05		
	16. Casse Dent			-2.210	<0.05
Edentulina moreleti	5. Gratte Fesse			-2.998	<0.01
Imperturbatia constans	15. La Reserve	-2.431	<0.05		
Glabrennea gardineri	2. MonPlaisir	-2.232	<0.05		
	7. Pisonia forest	-2.322	<0.05		
	8. Mont Dauban			-2.311	<0.05
Glabrennea silhouettensis	8. Mont Dauban	-3.002	<0.01		
Priodiscus serratus	2. Mon Plaisir			-2.091	<0.05
Seychellaxis souleyetianus	10. Congo Rogue	2.333	<0.05		
	15. La Reserve	-2.495	<0.05		
Silhouttia silhouettae	7. Pisonia forest	-2.112	<0.05	-2.188	<0.05
Stereostele nevilli	2. MonPlaisir			-2.387	<0.05
	7. Pisonia forest	-2.501	<0.05		
	10. Congo Rogue	-2.451	<0.05		
	13. Copolia	-2.500	<0.05	-2.451	<0.05
Nesokaliella minuta	17. Morne Blanc	-2.887	<0.01		
Pachnodus kantilali	10.Congo Rogue	-2.903	<0.01		
	17. Morne Blanc	-2.869	<0.01	-2.331	<0.05
Pachnodus niger x velutinus	10. Congo Rogue	-2.198	<0.05		
	13. Copolia	-2.220	<0.05	-2.098	<0.05
	16. Casse Dent	-2.433	<0.05	-2.337	<0.05
	17. Morne Blanc	-2.865	<0.01	-2.438	<0.05
	18. Mare aux Cochons	-2.199	<0.05		
Pachnouds ornatus	15. La Reserve	-2.267	<0.05		
Pachnodus velutinus	10. Congo Rogue	-2.355	<0.01		
Stylodonta unidentata	3. Jardin Marron			2.122	<0.05
	7. Pisonia forest	-2.410	<0.05	-2.191	<0.05

Table 1. (continued)

		1990 vs 2000		2000 vs 210	
		T	P	T	P
Stylodonta unidentata	10. Congo Rogue	-2.322	<0.05		
	14. Mont Sebert	-2.210	<0.05		
	15. La Reserve	-2.102	<0.05		
	17. Morne Blanc	-2.112	<0.05		
	18. Mare aux Cochons	-2.433	<0.05		
Leptichnodies verdcourti	16. Casse Dent	2.322	<0.05	3.155	<0.01

Table 2. MANCOVA of snail species abundance and environmental variables

Species	Variable	Df	SS	MS	F	P
Moominia willii	Cinnamomum	9	71.39	7.93	0.63	NS
	Q1 rain	1	207.86	207.86	16.51	<0.001
	Error	29	365.11	12.59		
	Total	39	644.36			
Augustula braueri	Cinnamomum	9	1608.03	178.67	2.23	<0.05
	Q1 rain	2	642.56	321.28	4.01	<0.05
	Error	78	6290.70	80.12		
	Total	89	8541.29			
Edentulina moreleti	Cinnamomum	9	159.21	27.69	2.15	NS
	Q1 rain	1	233.77	233.77	18.15	<0.001
	Error	29	244.72	12.88		
	Total	39	637.70			
Glabrennea gardineri	Cinnamomum	9	1820.61	202.29	2.62	<0.05
	Q1 rain	2	659.38	329.69	4.27	<0.05
	Error	87	6717.27	77.21		
	Total	89	9197.26			
Glabrennea silhouettensis	Cinnamomum	9	285.75	31.75	2.25	NS
	Q1 rain	2	325.38	162.69	11.53	<0.001
	Error	18	253.98	14.11		
	Total	29	865.11			
Priodiscus serratus	Cinnamomum	9	937.63	104.18	1.55	NS
	Q1 rain	2	642.52	321.26	4.78	<0.05
	Error	78	5242.38	67.21		
	Total	89	6822.53			
Nesokaliella minuta	Cinnamomum	9	1292.58	143.62	2.55	<0.05
	Q1 rain	2	1003.62	501.81	8.91	<0.01
	Error	48	2703.36	56.32		
	Total	59	4999.56			
Pachnodus kantilali	Cinnamomum	9	153.27	17.03	2.69	<0.05
	Q1 rain	2	184.82	96.41	15.23	<0.001
	Error	48	303.84	6.33		
	Total	59	641.93			
Pachnodus nigerxvelutinus	Cinnamomum	9	1464.12	162.68	1.98	NS
	Q1 rain	2	802.18	401.09	4.88	<0.05
	Error	78	6410.82	82.19		
	Total	89	8677.12			
Pachnodus oxoniensis	Cinnamomum	9	1306.62	145.18	1.65	NS
	Q1 rain	2	1036.52	518.26	5.89	<0.01
	Error	78	6863.22	87.99		
	Total	89	9206.36			
Pachnodus velutinus	Cinnamomum	9	183.06	20.34	2.23	NS
	Q1 rain	1	127.77	127.77	14.01	<0.01
	Error	9	82.08	9.12		
	Total	19	392.91			
Stylodonta unidentata	Cinnamomum	9	2518.92	249.88	2.22	<0.05
	Q1 rain	2	731.14	365.57	3.23	NS
	Error	288	32417.28	112.56		
	Total	299	35667.34			

Fig. 2. Changes in snail populations: alien and native species change in relation invasive plant abundance (proportion of trees identified as introduced). Bar charts: abundance of alien (blue) and native (red) snails, with standard errors of means. Map: levels of invasion coloured grey - suburban areas, green >60% invasives, blue 40-60%, yellow 25-40%, red <25%.

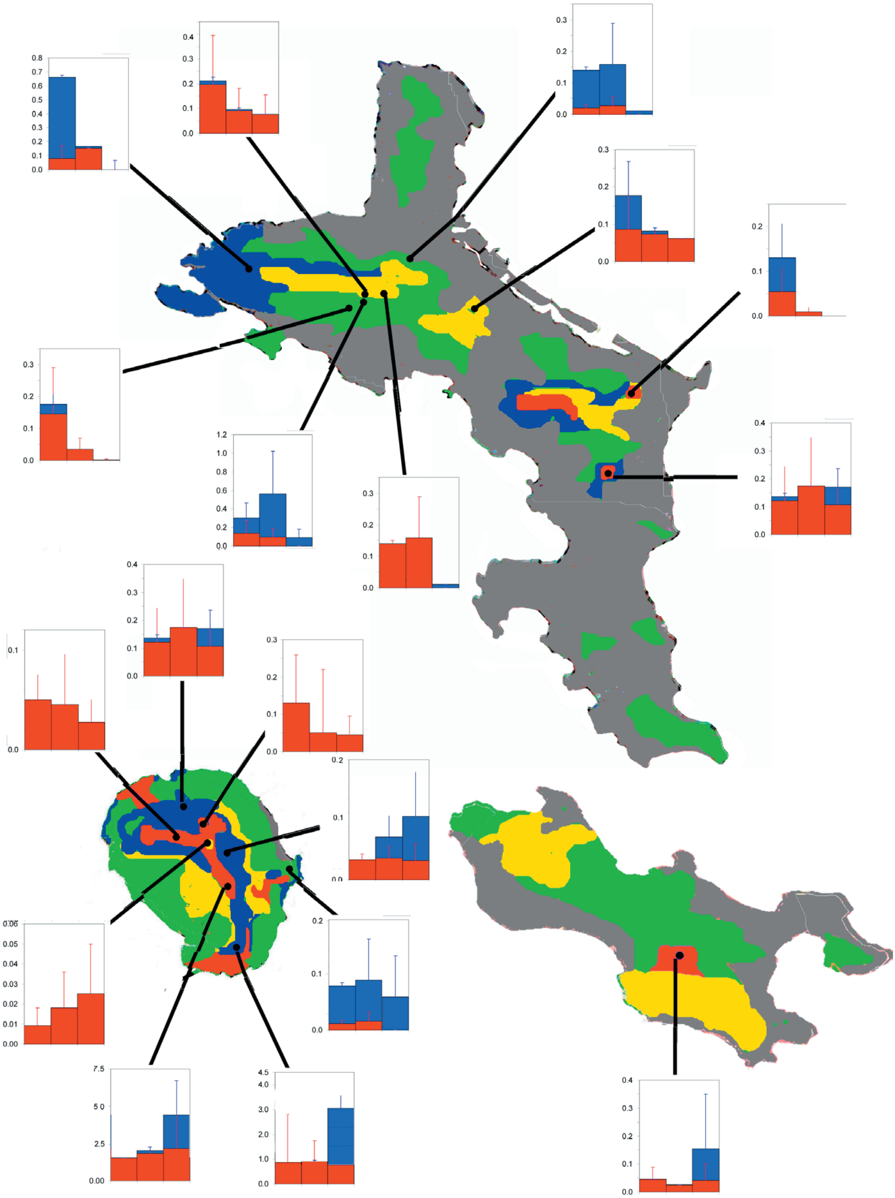
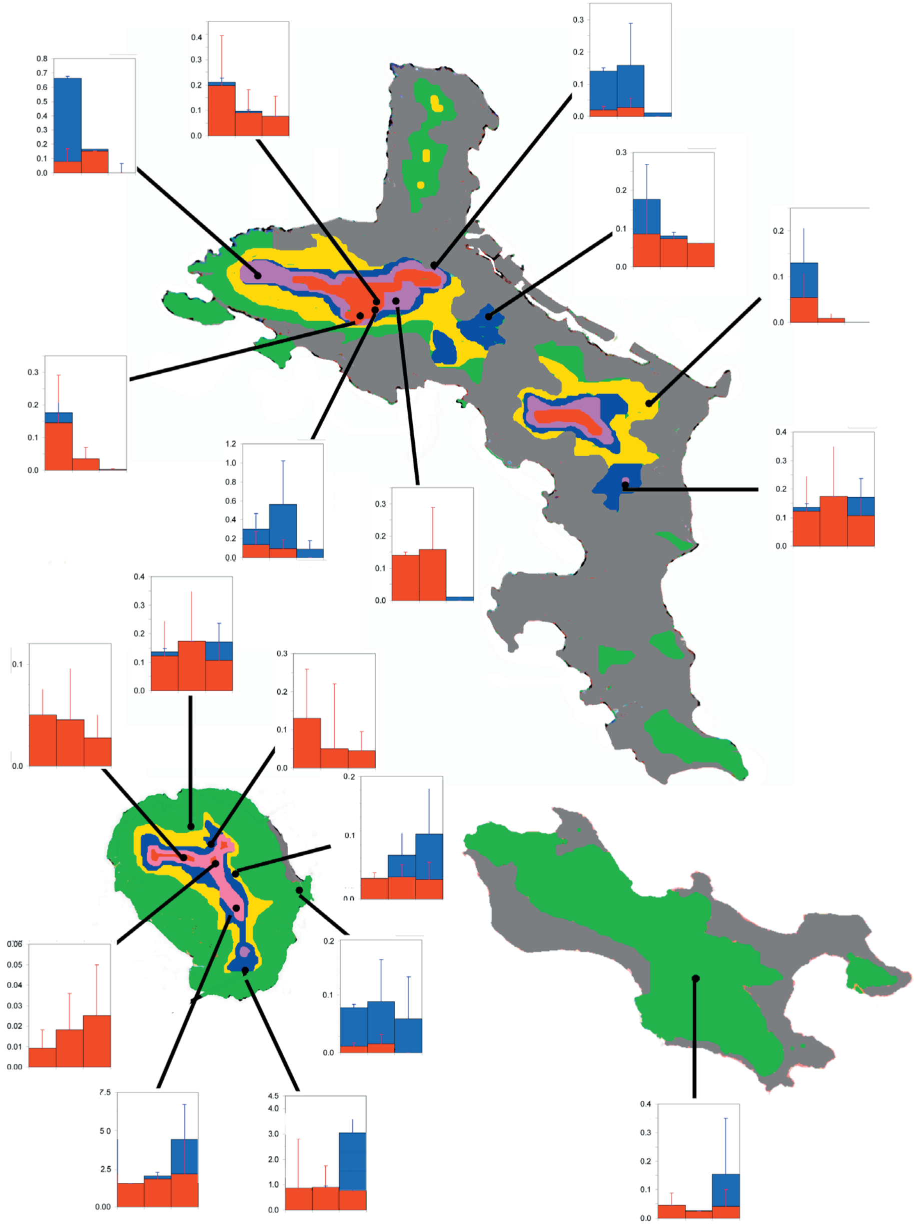


Fig. 3. Changes in snail populations: alien and native species change in relation to altitude (and climate change risk). Bar charts as Fig. 3. Map: grey – suburban; green <300m (low risk); yellow 300-400m, blue 400-500m; purple 500-550m; red >550m (high risk).



in the *Pisonia* forest and Mont Dauban in 1990 but not subsequently in either locality (Fig. 4c). *G. silhouettensis* was discovered in 1990 in a small area of Mont Dauban. It was recorded in the same locality in 1991 at lower densities, but has not been located since despite careful searching of the type locality and comparable areas in 2000, 2009 and 2010 (Fig. 4d). It is considered to be extinct. *Nesokaliella* showed rapid decline in *N. minuta* at Morne Blanc from 1988-1990; it was not recorded subsequently (Fig. 4e). In 2011 only one population was located (Praslin NP). These species were all significantly affected by rainfall but not invasive plants (Table 2).

The most significant declines were found in species of the genus *Pachnodus*. *Pachnodus* species at high altitude on Mahé declined rapidly from 1986-8 to 1991 for *P. velutinus* and *P. kantilali* (Fig. 4f & 4i). *P. nigerxvelutinus* also declined but at a slower rate (Fig. 4g). *Pachnodus* species at mid-high altitude on Mahé declined steadily from 1986, with decline most apparent from 1990. The lower altitude species on Mahé and on Praslin remained stable. On Silhouette rapid declines were recorded between 1990 and 2000 for high altitude *P. oxoniensis* (Fig. 4h) and *P. lionneti* in the *Pisonia* forest. The significantly declining species were all significantly affected by rainfall, and to a lesser extent invasive plants.

Stylodonta unidentata declined significantly in association with plant invasion, but not rainfall. These declines were only significant at Morne Blanc, Congo Rouge and Mare aux Cochons – Fig. 4j); non-significant declines were recorded at Mont Sebert and at La Reserve. One population increased in density; at Jardin Marron an increase was recorded following habitat restoration. These changes match habitat changes with notable declines in deteriorating sites, non-significant declines in stable sites and increases in the one restored site.

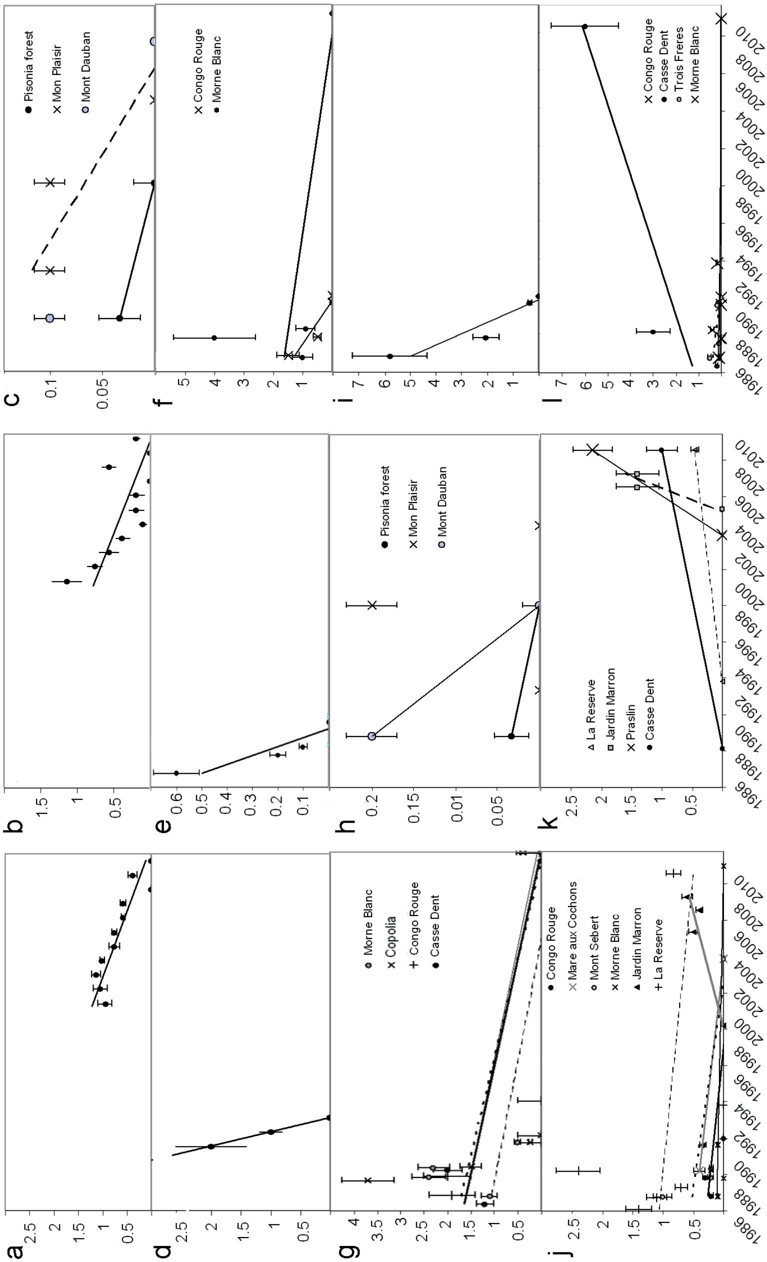
Increasing species (*Subulina striatella* and *Leptichonides verdcourti*) were not significantly affected by rainfall or plant species (Fig. 4k-l).

Habitat change

Significant changes in native and introduced plant densities are shown in Table 3. Tree density did not change at Trois Freres, Copolia, Praslin NP and the *Pisonia* forest, but a change in the balance between natives and invasives was apparent at Copolia where native seedlings decreased in abundance. Increases in invasion were apparent at Congo Rouge, Morne Blanc, La Reserve, Mon Plaisir and Mont Dauban. At Congo Rogue and Morne Blanc native seedling abundance also declined, and only invasive seedlings were recorded at Mont Dauban and Mon Plaisir. The only site with an increase in native trees and a decline in invasives was Jardin Marron, due to active management at this site from 2000-2010. At this site seedling abundance fluctuated significantly due weeding of invasives. Mon Plaisir showed increase in invasives but also an increase in natives due to regeneration of this site from a period of open habitat in 1990-2000. There is no general geographical pattern to habitat change, local factors (e.g. historical distribution of plantations) affecting forest dynamics.

Light level differences are shown in Fig. 5; relative light levels are calculated by dividing the recorded values by the average for that site.

Fig. 4. Changes in snail populations. a) *Moominia willii*; b) *Edentulina moreleti*; c) *Glabrennea gardineri*; d) *G. silhouettensis*; e) *Nesokaliella minuta*; f) *Pachnodus kantilali*; g) *P. nigerxvelutinus*; h) *P. oxoniensis*; i) *P. velutinus*; j) *Stylodonta unidentata*; k) *Subulina striatella*; l) *Leptichnoides verdcourti*



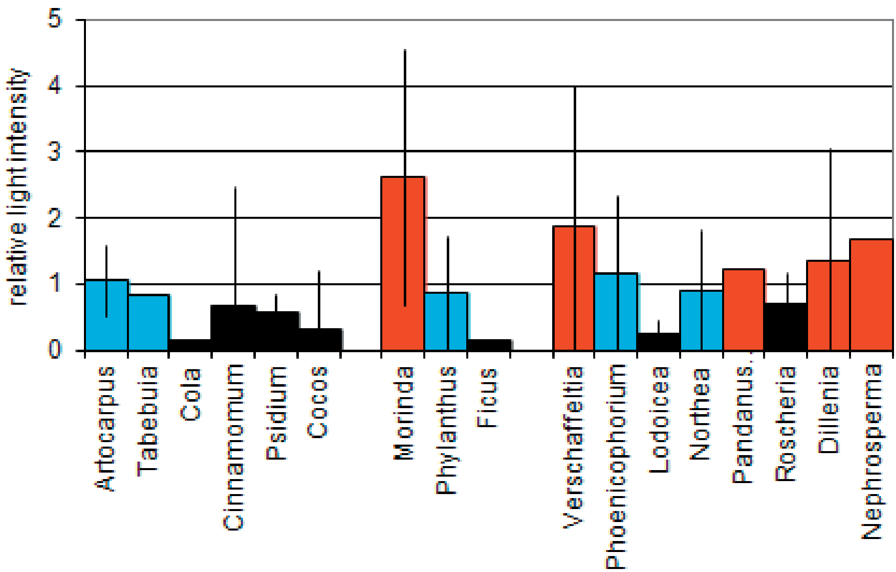
Climate change

No significant temperature changes were identified during the study period. Annual rainfall totals also did not change significantly but there was a notable change in rainfall seasonality, with a significant decline in rainfall in the first three months of the year (Fig. 6). The longest run of years with dryer than average first quarters was 2003-2011.

Table 3. Significant changes in native and invasive plant abundance between 1986-2012 and 1990-2012, T-test results with 19 degrees of freedom.

Locality	Tree changes				Seedlings			
	Natives		Invasives		Natives		Invasives	
	T	P	T	P	T	P	T	P
2. Mon Plaisir	2.111	<0.05	-3.001	<0.01	-2.879	<0.01	3.160	<0.01
3. Jardin Marron	2.978	<0.01	-3.121	<0.01			-2.395	<0.05
10. Congo Rogue			2.998	<0.01	-3.002	<0.01		
11. Trois Freres	-2.201	<0.05			2.132	<0.05		
12. Mission			2.405	<0.05			2.912	<0.01
13. Copolia			2.322	<0.05	-2.444	<0.05		
15. La Reserve	-2.199	<0.05	3.005	<0.01	2.501	<0.05	3.101	<0.01
17. Morne Blanc	-2.343	<0.05	3.100	<0.01			4.007	<0.001

Fig. 5. Relative light levels under different tree species, grouped as invasives (left 6), indigenous (centre 3) and endemic (right 8). Relative light levels coloured black <0.8, blue 0.8-1.2, red >1.2.



Discussion

The significant changes in snail populations could be divided into three categories: fluctuating species (with no clear pattern over the study period), increasing species and declining species. The most notable fluctuating species was *Pleuropoma theobaldiana*. This declined in one site from 1986-2012 (Morne Blanc) but has fluctuated, with periods of population increase and of decline, at five other sites (Copolia, Congo Rouge and La Reserve, *Pisonia* forest and Praslin NP). These sites cover a range of altitudes and are on different islands, with no identified common factors. The decline at Morne Blanc may be associated with the extreme habitat deterioration at this site, with populations at the other sites reflecting more normal unstable population dynamics in this species. In addition three of the carnivorous Streptaxidae show population increases in some sites and decreases in others and are also regarded as fluctuating. *Edentulina dussumieri* declined at La Reserve in the 1990s, and at Casse Dent in the 2000s, but increased in all periods in the *Pisonia* forest. *Seychellaxis souleyetianus* declined in the 1990s at La Reserve but increased in the same period at Congo Rouge. *Stereostele nevilli* declined at Congo Rouge and the *Pisonia* forest from 1990 but showed extreme fluctuations at Copolia. These are the three largest and most abundant streptaxids and population sizes probably reflect changes in the diverse prey species they consume.

Two species showed consistent population increases. *Subulina striatella* increased in the 2000s at six sites (Casse Dent, Gratte Fesse, Jardin Marron, Silhouette's south peak and in Praslin NP). *Leptichnoides verdcourti* increased in all periods at Casse Dent, in addition this species was found commonly at La Reserve for the first time in 2011, although not in any quantified samples. Both species were introduced to the islands in the 20th century; *S. striatella* first recorded in 1962 and *L. verdcourti* in 1986 (Gerlach 2006). These two species seem to be in a phase of active population expansion, with range expansion being apparent in *S. striatella* and *L. verdcoruti* increasing in abundance in higher-altitude sites where it was rare in the 1980s (Fig. 7).

Fig. 6. First quarter rainfall anomaly

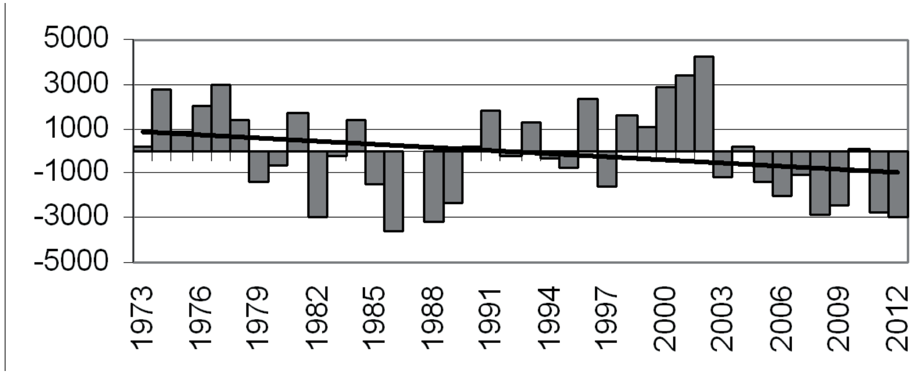
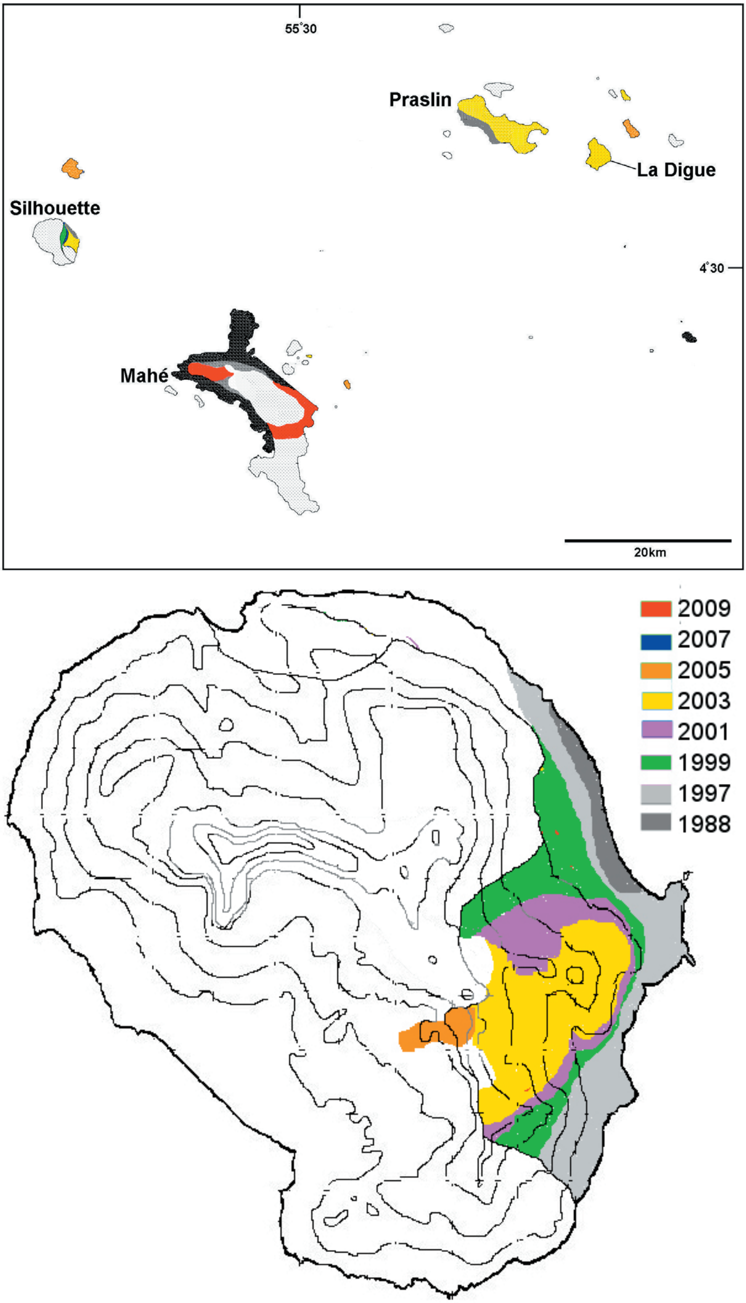


Fig. 7. Range expansion in *Subulina striatella*. Top – distribution in the granitic islands; bottom – distribution on Silhouette island. The species also colonised Denis and D'Arros by 2003



Of the 10 species that declined, the species that declined across their ranges are all high altitude species (*Moominia willii, Edentulina moreleti, Glabrennea gardineri, G. silhouettensis, Nesokaliella minuta, Pachnods velutinus, P. kantilali, P. oxoniensis*), species which declined in only some sites are more varied in their altitude adaptations, and declines were recorded in their highest altitude sites. The genus *Nesokaliella* covers a range of altitudes, with rapid declines in the high altitude *N. minuta* which was restricted to deteriorating habitat, and in *N. intermedia* on Silhouette which declined in all areas, irrespective of habitat quality. A third species, *N. subturritula*, is the most widespread species of the genus and occurs at lower altitudes than the others, declines were not recorded in this species.

Declines in the populations of Seychelles snails can be attributed to two main causes: habitat deterioration and climate change. Habitat deterioration includes changes in forest characteristics, as indicated by the data showing increasing depth of shade cast by the main invasive species (such as *Cinnamomum verum*). This would change the conditions in the leaf litter, affecting litter-dwelling snails and, more obviously, would affect the epiphyte flora and the associated arboreal organisms. Habitat appears to be the primary factor affecting *Stylodonta unidentata* and is a contributory factor for *Augustula braueri* (but only locally), *Glabrennea gardineri, Nesokaliella minuta* and *Pachnodus kantilali*. Climate is a significant factor affecting the high-altitude specialist species (*Moominia willii*, Streptaxidae and *Pachnodus* species). *Nesokaliella* may be affected by a combination of both factors, the most significant declines being found in *N. minuta* which occurs at high altitude in the most seriously deteriorating sites on Mahé island. The fact that *N. intermedia* has declined even in areas with improving habitat suggests that climate is a significant factor. It is probable that recorded declines in *Pachnodus* species are due to a combination of both factors. Climate has a major impact on Seychelles snail populations through rainfall patterns affecting recruitment; hatchlings of *Pachnodus* species require high levels of humidity (>90% at all times – pers. obs.). If low humidity occurs adults of most species (except the extinct *P. velutinus* – Gerlach 1996) enter aestivation and can tolerate hours, or days of relatively dry conditions. Lowland species can survive several weeks in this state. Hatchlings and small juveniles however are unable to do this and die within hours of humidity dropping below 90%. This means that prolonged dry periods will result in high levels of juvenile mortality, affecting population structure. Non-arboreal species would be better able to withstand dry conditions, the deeper layers of litter retaining moisture for longer, thus fewer terrestrial species show population declines. Those that are in decline are the most high-altitude specialist species (e.g. *Glabrennea* spp.). Mid- to low-altitude species are adapted to variable climates with periods of low humidity. They are thus more tolerant of the dry conditions that are associated with the decline of the high altitude species.

Until recently the forest ecosystems of the Seychelles islands were relatively intact and documented extinctions were attributed to direct hunting (birds, crocodiles and tortoises: Stoddart 1984) or to early lowland forest clearance (the snails *Pachndous ladiguensis* and *P. curiosus*: Gerlach 2006). The synergistic interaction of accelerating alien plant invasion (Kueffer *et al*. 2004; 2010) and climate change are now causing significant declines in high-forest species. Climate change is expected to combine

with habitat loss and fragmentation to increase species loss (Schindler 2001; Opdam & Wascher 2004; Brook *et al*. 2008). Climate change risk is greatest for isolated or fragmented populations that are unable to move in response to changing climates (Brook *et al*. 2008). The forest habitats of the Seychelles habitats are not highly fragmented but the high-altitude habitats are isolated and small in area, in addition snails have low mobility and so may be at particular risk. Whether or not Seychelles snail populations have experienced similar declines in the past as a result of natural climatic fluctuations is not known. There is no palaeoecological record comparable to that used to demonstrate prehistoric droughts in Mauritus (Van der Plas *et al*., 2012). Even if prolonged dry conditions do occur as part of natural processes present day populations may be particular prone to extinction risk due to the impacts of habitat degradation caused by invasive species and population fragmentation resulting from both habitat change and development.

Invasion may also be increasing due to the effects of climate change (Van der Wal *et al*., 2008; Mantyaka-pringle *et al*. 2012), although this has not been investigated in Seychelles. With a largely stable equatorial climate and only a recent human history (human settlement dating from 1772) the Seychelles islands are unlikely to be unusually vulnerable to these factors. Accordingly, it is to be expected that synergistic impacts of habitat deterioration and climate change will be occurring throughout the world. Further monitoring of invertebrate populations is needed to evaluate how significant these are elsewhere. Monitoring of snail populations is recommended due to their slow movement, easy detection and comparatively easy identification.

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